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On the commercial shrimps of the "*Parapenaeopsis cornuta* (Kishinouye, 1900)" species group (Crustacea, Decapoda, Penaeidae)

Tin-Yam Chan[1], Chien-Hui Yang[1], Appukttannair Biju Kumar[2], Amirah Hurzaid[3]

1 *Institute of Marine Biology and Center of Excellence for the Oceans, National Taiwan Ocean University, Keelung 202301, Taiwan*

2 *Department of Aquatic Biology & Fisheries, University of Kerala, Thiruvananthapuram 695581, Kerala, India*

3 *Biological Sciences Department, School of Distance Education and School of Biological Sciences, University Sains Malaysia, 11800 Minden, Penang, Malaysia*

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Corresponding authors: Chien-Hui Yang (chyang@ntou.edu.tw); Amirah Hurzaid (amirahhurzaid@usm.my)

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Abstract

Penaeid shrimps belonging to the *Parapenaeopsis cornuta* (Kishinouye, 1900) species group hold significant commercial value in the Indo-West Pacific, but their taxonomy has been problematic. A taxonomic revision of this group, supported by molecular genetic analysis using the barcoding gene COI, confirmed the validity of all four species within the group. Their distinguishing characteristics are redefined and illustrated, and a key for identifying the four species in the "*P. cornuta*" group is provided.

Key Words

DNA barcode, marine, molecular, revision, taxonomy

Introduction

The moderate small penaeid shrimp (body length excluding rostrum about 10 cm), *Parapenaeopsis cornuta* (Kishinouye, 1900), is generally considered to be widely distributed in the Indo-West Pacific (Japan to India and Australia) and fished commercially in some areas (Chan 1998; Holthuis 1980; 1984; Liu and Zhong 1988; Yu and Chan 1986). This species, however, has a lot of taxonomic ambiguities (also see Hsu and Chan 2023). A very similar species, *P. maxillipedo* Alcock, 1906, was described from India and also considered to be widely distributed in the Indo-West Pacific, but with a more southern distribution from India to the Philippines and Australia (Chan 1998; Holthuis 1980; 1984; Pérez Farfante and Kensley 1997). Alcock (1906), in his original description of *P. maxillipedo*, suspected that this species may belong to the same species as *P. cornuta*. Some later workers had synonymized these two names or treated them as subspecies (e.g., Dall and Rothlisberg 1990; Racek and Dall 1965; Racek and Yaldwyn 1971). Liu and Wang (1987) split the Chinese material of *P. cornuta* into three species with the erections of *P. sinica* Liu & Wang, 1987, and *P. incisa* Wang & Liu in Liu and Wang 1987 from southern China, without knowing that V. C. Nguyên (1971) had already named their *P. sinica* as *P. amicus* from Vietnam. Nevertheless, some workers (e.g., Dall and Rothlisberg 1990; Hayashi 1992) commented that the distinguishing characters proposed for *P. amicus* and *P. incisa* are too subtle and considered both names to be junior synonyms of *P. cornuta*. On the other hand, Sakai and Shinomiya (2011) erected a genus, *Kishinouyepenaeopsis*, for these four very similar species, namely *P. cornuta*, *P. maxillipedo*, *P. amicus*, and *P. incisa*. Recent molecular analysis by Hurzaid et al. (2020) even suggested that there may be more than eight species in *Kishinouyepenaeopsis*.

As commented in Hsu and Chan (2023), splitting of *Parapenaeopsis* Alcock, 1901 s. l. is not adopted because there are still many controversies on the status and nomenclature in separating *Parapenaeopsis* s. l. like the separation of the genus *Penaeus* Fabricius, 1798 (see Yang et al. 2023). For example, Sakai and Shinomiya

(2011) used only the differences of the petasma to split *Parapenaeopsis* into seven genera. Chanda (2016a, b) disagreed with such classification but created two more generic names in *Parapenaeopsis* s. l. Until there are better supports for those genera created by Sakai and Shinomiya (2011), the genus *Kishinouyepenaeopsis* is not recognized and treated as a junior synonym of *Parapenaeopsis*. The term "*P. cornuta*" species group is hence used to refer to these four closely related species.

Of the four species in the "*P. cornuta*" species group, *P. amicus* is quite different and rather easy to recognize (see Hsu and Chan 2023). This work, with the aid of DNA barcoding data, compared *P. cornuta*, *P. maxillipedo*, and *P. incisa* material from different areas, including their topotypic localities, as well as abundant specimens of *P. amicus* from Taiwan. The results showed that the four currently recognized names in the "*P. cornuta*" species group are all valid. The distinguishing characteristics of these four named species are redefined in order to facilitate the taxonomy of this species group if more taxa will be discovered later.

Materials and methods

Specimens examined are deposited in the National Taiwan Ocean University, Keelung (**NTOU**), Universiti Sains Malaysia, Penang (**USM**), Natural History Museum and Institute, Chiba, Japan (**CBM**), Marine Biological Museum of the Chinese Academy of Sciences, Qingdao (**MBM**). As members of the "*P. cornuta*" species group are widely distributed in the Indo-West Pacific and fished commercially in many areas, there are a lot of reports on them with abundant material deposited at many institutions worldwide. Nevertheless, most previous publications on this group did not state or illustrate explicitly the distinguishing characters used in this work and rendered their identities indeterminable. It was considered too major a task to examine all the material of this group around the world and to verify the identification of all previous records. The synonymy given, therefore, is restricted to important taxonomic literature of the species. To facilitate their identification by shrimp workers, a key as well as a table of distinguishing characters for the species of this group are herein provided. The measurements provided are carapace length (cl), which is measured dorsally from the posteriormost orbital margin to the posterior margin of the carapace (Fig. 2a). The length and width ratio of the anterior plate of the thelycum is measured as width = widest part, length = from widest part to most distal (or anteriormost) point (Fig. 5a). The terminology used mainly follows Chan (1998) with Hsu and Chan (2023). As there are a lot of specimens of *P. cornuta* and *P. amicus* deposited in NTOU (see Hsu and Chan 2023), the counts and measurements given in the "Diagnosis" and "Remarks" were randomly selected from five and 10 specimens of each sex of these two species for the Taiwanese material, respectively. All specimens from other localities were included for comparisons amongst species.

DNA barcodes (mitochondrial cytochrome c oxidase I gene, mtCOI, Hebert et al. 2003) were employed to determine the taxonomic status of *P. cornuta*, *P. maxillipedo*, *P. amicus*, and *P. incisa*. Specimens sequenced in this work are shown in Table 1. Crude genomic DNA was extracted from the fifth pleopod or the muscles of the abdomen using the DNeasy® Blood and Tissue Kit (Qiagen, Hilden, Germany) following the protocol of the manufacturer. The universal primer, LCO1490/HCO2198 (~657 bp, Folmer et al. 1994), was used for the sequence amplification. PCR reactions, cycling profiles (annealing temperature 47.8 °C for mtCOI gene), product checking, and sequencing procedures followed Yang et al. (2015). Output sequences were edited for contig assembly by SeqMan Pro™ (Lasergene®; DNASTAR, Madison, WI, USA) before being blasted on GenBank (National Center for Biotechnology Information, NCBI) to check if any potential contamination. EditSeq (Lasergene®; DNASTAR) was used to translate into the corresponding amino acid sequences to avoid the inclusion of pseudogenes for the COI dataset (Song et al. 2008). All mtCOI sequences from the "*P. cornuta*" species group reported by Hurzaid et al. (2020) were included in the analyses. Sequence alignment was performed by the MAFFT v. 7 online service (Katoh et al. 2019), and a nucleotide length of 615 bp was used in the final analyzed dataset. The two Taiwanese specimens of *P. cornuta* [NTOU M02358] did not achieve this nucleotide length and only had 612 and 470 bp. The gaps in these two shorter sequences were filled by the fifth nucleotide "N". Corrected pairwise distance was calculated based on the Kimura 2-parameter model (K2P; Kimura 1980) by MEGA v.11 (Tamura et al. 2021). A maximum-likelihood (ML) tree was constructed using the IQ-TREE web server (Trifinopoulos et al.

Table 1. Pairwise distance (%) based on the Kimura-2-parameter (K2P) model of partial mitochondrial COI sequences (615 bp) among four species of the "*Parapenaeopsis cornuta*" group in a dataset of sequences generated in this work plus three sequences of *P. amicus* from Taiwan in Hurzaid et al. (2020) with their specimens re-examined. Numbers in parentheses are sample sizes. GenBank numbers, see Fig. 8.

	P. cornuta (6- **J**, T, C)	***P. maxillipedo*** (7- **I**, M)	***P. amicus*** (3- T)	***P. incisa*** (2- **C**)
P. cornuta (6- **J**, T, C)	0.0–0.7			
P. maxillipedo (7- **I**, M)	13.5–16.0	0.0–0.7		
P. amicus (3- T)	14.2–17.5	19.7–20.6	0.2–0.5	
P. incisa (2- **C**)	15.0–17.5	19.3–20.7	20.4–20.9	0.0

J: Japan, T: Taiwan, C: Southern China, I: India, M: Malaysia.
Bold: type-locality of the species.

2016) with 1000 bootstrap replicates based on the model of "TIM2+G4+F" and with the congeneric species *P. hardwickii* (Miers, 1878) used as an outgroup.

Systematic account

Family Penaeidae Rafinesque, 1815
Genus *Parapenaeopsis* Alcock, 1901

Parapenaeopsis cornuta (Kishinouye, 1900)

Figs 1a, 2a, 3a, 4a, 5a, 6a, 7a, b

Penaeus cornutus Kishinouye 1900: 23, unnumbered text fig., p1. 7-figs 9, 9A (type locality: Ariake, Japan).

Parapenaeopsis cornutus – Kubo 1949: 374 (? in part–Taiwanese material), figs 7Z, 10B, 22I, 32C, D, 47N, 63A, B, 75F, L, 78L, 135C, 136A, B.

Parapenaeopsis cornuta – Hayashi 1986: 67, fig. 26; 1992: 105, fig. 57a-c; Liu and Wang 1987: 524, fig. 2; Liu and Zhong 1988: 208, fig. 129, pl. 6: 5; Hsu and Chan 2023: 224, figs 2, 6b.

Kishinouyepenaeopsis cornuta – Sakai and Shinomiya 2011: 499, figs 3A, B, 4F; De Grave and Fransen 2011: 216.

Material examined. **Japan** • [CBM ZC3280]: Tosa Bay, Katsura-hama Beach, commercial trawler, 10–20 m, 28 Nov. 1996, 3♂♂, cl 15.6–17.4 mm, 1 ♀, cl 19.0 mm • [NTOU M02640]: Aichi, Minami-Chita, Toyohama fishing port, commercial trawler, 18 m, 31 Oct. 2024, 1♂, cl 20.7 mm • [NTOU M02641]: Aichi, Nishio, Isshiki fishing port, commercial trawler, 22.5 m, 14 Dec. 2024, 1♂, cl 14.3 mm, 3♀♀, cl 21.5–24.6 mm.

Taiwan • [NTOU M02355]: Yilan County, Dasi fishing port, commercial trawler, 10 Mar. 1985, 2♂♂, cl 14.5–18.4 mm • [NTOU M02356]: Yilan County, Dasi fishing port, commercial trawler, 5 Aug. 1982, 1♂, cl 22.9 mm, 1♀, cl 28.9 mm • [NTOU M02357]: Keelung City, commercial trawler, 12 Oct. 1990, 1♂, cl 14.5 mm • [NTOU M02358]: Changhua County, Wenzi fishing port, commercial trawler, 5 Aug. 2021, 3♂♂, cl 16.6–17.4 mm, 39♀♀, cl 17.2–22.0 mm • [NTOU M02359]: Chiayi County, Budai fishing port, commercial trawler, 26 May 1974, 2♀♀, cl 18.0–18.7 mm • [NTOU M02360]: Chiayi County, Budai fishing port, commercial trawler, 20 Jan. 1995, 1♀, cl 18.2 mm • [NTOU M02485]: Chiayi County, Budai fishing port, commercial trawler, 2 Jul. 2002, 1♀, cl 13.6 mm • [NTOU M02361]: Kaohsiung City, Singda fishing port, commercial trawler, 24 Jul. 1984, 2♀♀, cl 16.1–17.0 mm • [NTOU M02362]: Kaohsiung City, Kaohsiung port, station 4, 1 Mar. 1994, 2♂♂, both cl 18.1 mm • [NTOU M02363]: Kaohsiung City, Cijin, 25 Mar. 1996, 4♂♂, cl 18.6–19.5 mm, 7♀♀, cl 19.1–23.1 mm • [NTOU M02364]: Pingtung County, Donggang fishing port, commercial trawler, 28 Jul. 1985, 2♂♂, cl 15.1–16.8 mm, 2♀♀, cl 19.2–19.3 mm • [NTOU M02419]: No specific data, 2♀♀, cl 21.1–21.2 mm • [NTOU M02486]: No specific data, 2♂♂, cl 19.0–19.2 mm, 2♀♀, cl 23.1–23.4 mm • [NTOU M02487]: No specific data, 1♂, cl 18.3 mm, 3♀♀, cl 16.2–22.8 mm.

Southern China • [MBM 155050]: Fujian, Xiamen fish market, 05F-16, 3 Sep. 2005, 2♂♂, cl 18.1–18.7 mm, 2♀♀, cl 19.4–22.3 mm • [MBM 155083]: Guangdong, Yangjiang, Zhapo, Dajiao hill, 54-K187B, 18 Nov. 1954, 2♂♂, cl. 14.3–17.7 mm, 2 ♀♀, cl 15.7–16.8 mm • [MBM 155080]: Hainan, Boao, stn 3, 8 Nov. 1990, 2♀♀, cl 12.0–16.3 mm • [MBM 155074]: Hainan, Sanya bay, stn 3, CJ97C-164, 3–4 m, Nov. 1997, 1♀, cl 18.1 mm.

Diagnosis. Rostrum more or less horizontal, straight, extending to distal segment of antennular peduncle and often reaching tip of antennular peduncle, armed with 6–8 (avg. 7.0, n = 27) dorsal teeth (excluding epigastric tooth), tip devoid of tooth and slightly curved upwards. Postrostral carina generally having a weak median pit and with posterior 1/4 broadened and obscure, extending posteriorly to 0.72–0.92 (avg. 0.85, n = 30) of carapace length. Longitudinal suture short and extending to about level of epigastric tooth. Pereiopods I and II with basial spines and epipods. Pereiopod III generally lacking basial spine, rarely a minute to small basial spine present only in males. Abdominal somites I and II lacking dorsal carina. Telson without lateral movable spinules. Males with endopod of pleopod II strongly modified into boot-like shape, distal margin straight or more often distinctly concave medially, anterodistal part bearing tuft of dense long stiff setae extending beyond distal margin; petasma lacking distomedian projection but with distolateral projections strongly elongated and horn-like, tip of horn distinctly protruded at outer side. Female thelycum with anterior plate mostly semi-quadrate to sometimes semi-circular and 0.74–0.95 (avg. 0.85, n = 16) as long as wide, anterior margin with median part occasionally slightly protruded, surface slightly sunken and rarely with median longitudinal furrow; posterior plate with weak median ovate boss, lateral parts as large semicircular process; tuft of setae behind posterior plate long and thick.

Coloration. (Fig. 7a, b) Body generally greenish to bluish gray and densely covered with dark green dots. Antennal flagellae and abdomen slightly banded. Tip of rostrum dark brown to reddish brown. Eyes black gray. Uropods of tail fan dark green to dark red and with yellowish margins. Thoracic appendages pinkish white. Pleopods with rami reddish. Tuft of long setae behind thelycum bluish. Color photographs verified belonging to this species are provided by Hayashi (1986: fig. 26) and Hsu and Chan (2023: fig. 6b).

Distribution. Known with certainty from Japan to Taiwan and southern China, intertidal to 32 m deep (Liu and Zhong 1988). Perhaps more widely distributed west to India and south to northern Australia (see Remarks).

Remarks. For those distinguishing characters found in this study to be useful in separating the species of the "*P. cornuta*" group (Figs 1–6, Table 2), topotypic material of *P. cornuta* from Japan has the pereiopod III generally lacking a basial spine; postrostral carina with the posterior part faded and extending to a position with a distinct distance from the posterior margin of the carapace; male pleopod II with endopod boot-like and having the distal margin straight or medially concave; petasma with tip of horn distinctly protruded only at the outer side; thelycum

with anterior plate generally semi-quadrate and slightly shorter than width; posterior plate bearing a weak median ovate boss and a tuft of long setae behind it. Specimens with the above characteristics from Japan [CBM ZC3280, NTOU M02641], Taiwan [NTOU M02358], and southern China [MBM 155074] have 99.3–100% similarity in the barcoding mtCOI gene (615 bp, Table 1) and can be safely considered as belonging to the same species. Of the 100 specimens (including 27 males) examined, only two males from Japan [CBM ZC3280] and Taiwan [NTOU M02356] have their pereiopods III bearing small basial spines (on both sides). As the median boss at the posterior plate of the thelycum is weak in this species, this boss is sometimes rather rudimentary in small females.

Although *P. cornuta* can be readily separated from the other species of the "*P. cornuta*" species group by a combination of characters (Table 2), it does not have a unique and conspicuous distinguishing character. Its number of rostral teeth, shape of the postrostral carina, pereiopod III lacking an basial spine and even body coloration are nearly identical with *P. amicus* and *P. incisa* (exact coloration still unknown). The petasma and boot-like endopod of the pleopod II in males, as well as the shape of the anterior plate of the thelycum and the tuft of hairs (including color of hairs) behind the thelycum, are almost the same between *P. cornuta* and *P. maxillipedo* (Figs 3a, b, 4a, b, 5a, b). Only the median boss at the posterior plate of the thelycum is relatively lower (Fig. 5a) than that of *P. maxillipedo* (Fig. 5b), while the median part of the posterior plate is flattened or sunken in *P. incisa* (Fig. 5d) and *P. amicus* (Fig. 5c), respectively. Nevertheless, the characteristic shape of the thelycum is generally underdeveloped in small females of penaeids. Therefore, the posterior plate of the thelycum is very similar amongst small females of *P. cornuta*, *P. maxillipedo*, and *P. incisa*.

The lack of a unique, conspicuous character to distinguish *P. cornuta* from the other species of the "*P. cornuta*" group renders the verification of the distribution records of this species very difficult. The original description of *P. cornuta* (Kishinouye 1900) also has not mentioned nor illustrated clearly the present distinguishing characters used for separating the species of the "*P. cornuta*" group. The whereabouts of the type of *P. cornuta* is not known, and it is not in the National Museum of Nature and Science, Tokyo (personal communication from Tohru Naruse) or the University of Tokyo (where Kishinouye studied, personal communication from Tomoyuki Komai). Nevertheless, there is no report nor evidence that there is more than one species of the "*P. cornuta*" group present in Japan (see Hayashi 1986, 1992; Kubo 1949). Thus, the Japanese specimens examined in this work can be treated as typical *P. cornuta*.

It has been considered that *P. cornuta* is widely distributed in the Indo-West Pacific from Japan to India and tropical Australia (see Chan 1998; Holthuis 1980, 1984; Pérez Farfante and Kensley 1997). Other than its records from Taiwan and southern China confirmed by the present material examined, reports of this species from other areas need verification. For example, there is the possibility that the photographs assigned to "*P. cornuta*" from Thailand (Chaitiamvong and Supongpan 1992: pl. 44) and Australia (Grey et al. 1983: fig. 39) may actually represent *P. amicus* or *P. incisa* as some molecular analyses (Hurzaid et al. 2020; Fakhruddin et al. 2024) have already suggested that *P. incisa* is likely at least ranging to the Strait of Malacca or even to Bangladesh (see "Discussion" below).

Parapenaeopsis maxillipedo Alcock, 1906

Figs 1b, 2b, 3b, 4b, 5b, 6b, 7c

Parapenaeopsis maxillipedo Alcock 1906: 40, pl. VIII–fig. 24, 24a–b (type-locality: Bombay and Madras, India and Arakan, Myanmar); Holthuis 1984: PEN Para 8, 4 unnumbered figs; De Bruin et al. 1995: 32, 3 unnumbered figs; Chan 1998: 944, 3 unnumbered figs.

Parapenaeopsis (*Kishinouyepenaeopsis*) *maxillipedo* – Psomadakis et al. 2019: 39, 4 unnumbered figs.

Kishinouyepenaeopsis maxillipedo – De Grave and Fransen 2011: 216.

Material examined. **India** • [NTOU M02625]: Tamil Nadu, Tuticorin fishing harbor, commercial trawler, 18 Mar. 2017, 2♂♂, cl 14.4–16.0 mm, 3♀♀, cl 11.4–22.3 mm • [NTOU M02626]: Tamil Nadu, Tuticorin fishing harbor, commercial trawler, 22 Mar. 2017, 1♂, cl 11.9 mm, 1♀, cl 19.0 mm • [NTOU M02627]: Tamil Nadu, Tuticorin fishing harbor, commercial trawler, 22 Mar. 2017, 1♂, cl 12.1 mm, 1♀, cl 15.4 mm • [NTOU M02628]: Muttom, Jeppiaar fishing harbor, commercial trawler, Sep. 2018, 2♂♂, cl 13.9–14.0 mm. **Malaysia** • [USM_INV1006]: Strait of Malacca, Pantai Remis, Perak, 10 Aug. 2023, 1♂, cl 18.6 mm • [USM_INV1009]: Strait of Malacca, Pantai Remis, Perak, 10 Aug. 2023, 1♂, cl 22.5 mm • [USM_INV1010]: Strait of Malacca, Pantai Remis, Perak, 10 Aug. 2023, 1♂, cl 18.9 mm • [USM_INV1011]: Strait of Malacca, Pantai Remis, Perak, 10 Aug. 2023, 1♀, cl 26.8 mm • [USM_INV1012]: Strait of Malacca, Pantai Remis, Perak, 10 Aug. 2023, 1♀, cl 25.7 mm.

Diagnosis. Rostrum generally straight and horizontal, reaching between base and middle of distal antennular peduncle segment, bearing 8–10 (avg. 8.9, n = 15) dorsal teeth (excluding epigastric tooth), tip without tooth, and slightly curved upwards. Postrostral carina distinct and similar width along entire length but often with a weak median pit, almost reaching posterior margin of carapace and being 0.91–0.97 (avg. 0.96, n = 16) of carapace length. Longitudinal suture short and extending to about level of epigastric tooth. Pereiopods I and II bearing basial spines and epipods. Pereiopod III generally armed with distinct basial spine. Abdominal somites I and II without dorsal carina. Telson without movable lateral spinules. Males with endopod of pleopod II strongly modified into boot-like shape, distal margin straight or slightly concave medially, median part of distal margin concealed by tuft of dense long stiff setae arose from anterodistal part of endopod; petasma horn-like with distolateral projections strongly elongated, tip of horn bearing distinct protuberance only at outer side. Female thelycum, anterior plate generally semi-quadrate or sometimes semi-circular, 0.79–1.03 (avg. 0.91, n = 7) as

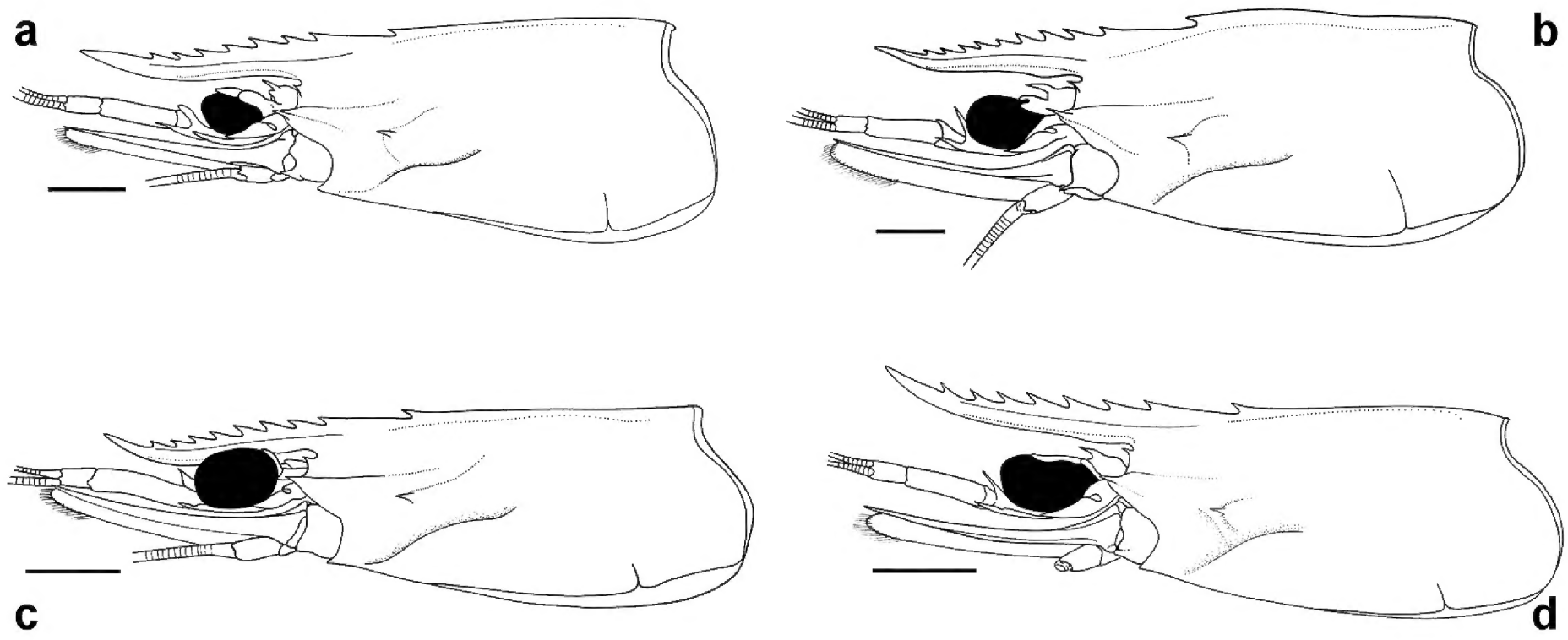

Figure 1. Carapace and anterior appendages, lateral view. **a.** *Parapenaeopsis cornuta* (Kishinouye, 1900), Cijin, Kaohsiung City, Taiwan, female cl 22.4 mm (NTOU M02363). **b.** *P. maxillipedo* Alcock, 1906, Strait of Malacca, Pantai Remis, Perak, Malaysia, female cl 26.8 mm (USM_INV 1011). **c.** *P. amicus* V. C. Nguyên, 1971, Budi fishing port, Chiayi County, Taiwan, female cl 27.3 mm (NTOU M02372). **d.** *P. incisa* Wang & Liu in Liu and Wang 1987, Sanya, Hainan, Southern China, females cl 17.6 mm (MBM 155044). Scale bars: 5 mm.

long as wide, surface slightly sunken and lacking median longitudinal furrow; posterior plate with distinct and often high median ovate boss, lateral parts semicircular; tuft of setae behind posterior plate long and thick.

Coloration. (Fig. 7b) Body greenish yellow and covered with dense yellowish to dark green dots. Eyes black gray. Antennal flagellae pinkish to yellowish and alternated with dark bands. Rostrum with tip reddish to dark reddish brown, bases of rostral teeth sometimes black and continuous as thick black line. Thoracic appendages whitish to pinkish white and greenish yellow. Abdomen with dense dark green dots arranged as distinct transverse bands, last somite (or somite VI) bearing a large black or brown posterolateral spot anteriorly accompanied with thick white margin. Uropods of tailfan reddish to dark red and with yellowish green margins or distal parts yellowish green. Pleopods pale white to pale yellow or reddish, outer parts of peduncles sometimes whitish. Tuft of long setae behind thelycum bluish. Color photograph belonging to this species given in Chaitiamvong and Supongpan (1992: pl. 43).

Distribution. Known with certainties from India to Thailand and Strait of Malacca, shallow water less than 30 m deep (Chan 1998). Perhaps more widely distributed eastwards to the Philippines and northern Australia (see Remarks).

Remarks. The relationships between *P. maxillipedo* and *P. cornuta* are extremely confusing in literature. *Parapenaeopsis maxillipedo* was suspected to belong to the same species as *P. cornuta* in the original description (Alcock 1906), and some authors also suspected or considered these two names to be synonyms (e.g., Dall 1957; Dall and Rothlisberg 1990; De Man 1911; Hall 1961). Other workers, however, considered that *P. maxillipedo* is a distinct species or subspecies (e.g., Chaitiamvong and Supongpan 1992; Chan 1998; Chanda 2016b; Holthuis 1980, 1984; Kubo 1949; Liu and Wang 1987; Liu and Zhong 1988; Motoh and Buri 1984; Muthu 1968; Racek and Dall 1965; Racek and Yaldwyn 1971) and proposed many characters to separate it from *P. cornuta*. Careful comparisons and molecular analyses of materials assigned to *P. maxillipedo* and *P. cornuta* in this work reveal that there are large nucleotide divergences (13.5–16.0%, Table 1) between these two species and they can be separated by the following characters.

As commented on by many workers (Chan 1998; Chanda 2016b; Dall 1957; De Man 1911; Hall 1961; Holthuis 1984; Kubo 1949; Liu and Wang 1987; Liu and Zhong 1988; Motoh and Buri 1984; Muthu 1968; Racek and Dall 1965; Racek and Yaldwyn 1971), the pereiopod III generally bears a distinct basial spine in *P. maxillipedo* (Fig. 6b) but lacks a basial spine in *P. cornuta* (Fig. 6a). Nevertheless, as pointed out by Kubo (1949) as well as Racek and Dall (1965), there are variations in this character. Of the 16 specimens (including nine males and seven females) of *P. maxillipedo* examined in this work, a male [NTOU M02625] and a female [NTOU M02627] from India lack a basial spine at the pereiopod III on both sides. Another female [NTOU M02625], also from India, only has a small basial spine at the pereiopod III. On the other hand, only two (both males) of the 100 specimens (including 27 males) examined in *P. cornuta* have small ischial spines present on the pereiopods III. The rostrum is generally shorter (maximum extending to the middle of the distal antennular segment) but armed with more teeth (8–10, avg. 8.9) in *P. maxillipedo* (Fig. 1b). The rostrum of *P. cornuta* (Fig. 1a) is relatively longer (maximum reaching tip of antennular peduncle) and bears fewer teeth (6–8, avg. 7.0). The postrostral carina is distinct along the entire length and almost reaches the posterior margin of

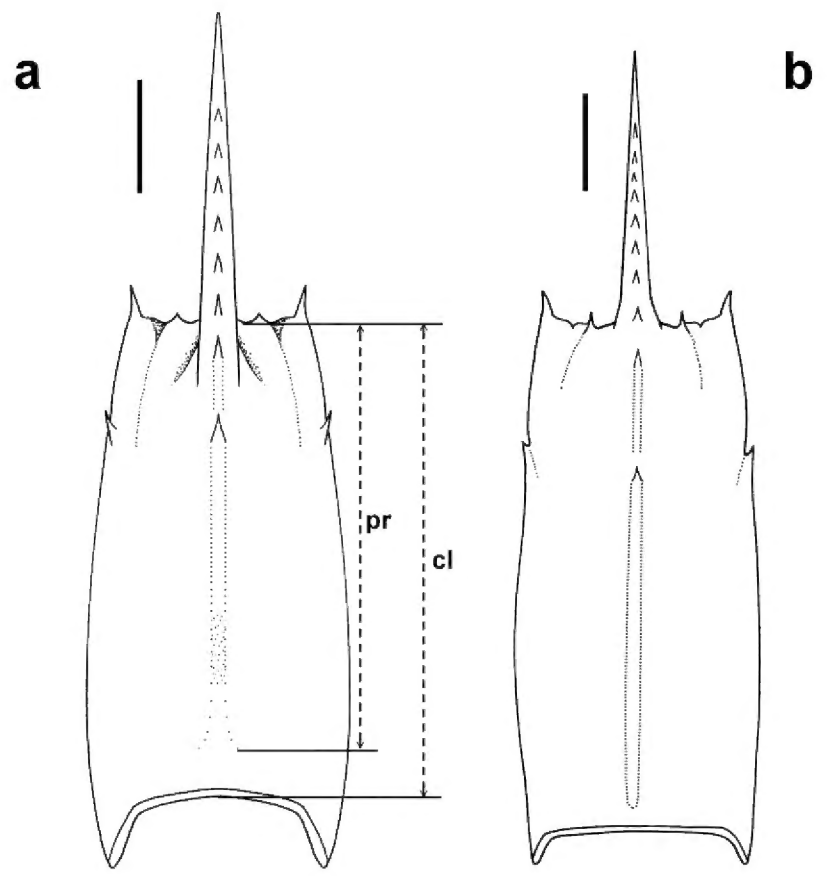

Figure 2. Carapace, dorsal view. **a.** *Parapenaeopsis cornuta* (Kishinouye, 1900), Cijin, Kaohsiung City, Taiwan, female cl 22.4 mm (NTOU M02363). **b.** *P. maxillipedo* Alcock, 1906, Strait of Malacca, Pantai Remis, Perak, Malaysia, female cl 26.8 mm (USM_INV 1011). **c.** *P. amicus* V. C. Nguyên, 1971, Budi fishing port, Chiayi County, Taiwan, female cl 27.3 mm (NTOU M02372). **d.** *P. incisa* Wang & Liu in Liu and Wang 1987, Sanya, Hainan, Southern China, females cl 17.6 mm (MBM 155044). pr: postrostral carina length; cl: carapace length. Scale bars: 5 mm.

the carapace (postrostral carina/cl: 0.91–0.97, avg. 0.96) in *P. maxillipedo* (Figs 1b, 2b), but it is faded and broadened at posterior 1/4 and terminates with a distinct distance from the posterior carapace (postrostral carina/cl: 0.72–0.92, avg. 0.85) in *P. cornuta* (Figs 1a, 2a). The median boss at the posterior plate of the thelycum is strongly elevated in *P. maxillipedo* (Fig. 5b) but weak in *P. cornuta* (Fig. 5a). However, as the development of the thelycum is related to size, the median bosses in some juveniles of *P. maxillipedo* are sometimes low and rather similar to that of *P. cornuta*. The most distinct difference between *P. maxillipedo* and *P. cornuta* is body coloration. Some of the Indian specimens and all Malaysian specimens of *P. maxillipedo* examined in this study are accompanied by color photographs showing the same color pattern. The abdomen is distinctly banded and bears a large dark spot with an anterior thick white margin on the lateral surfaces of the last somite in *P. maxillipedo* (Fig. 7c). In *P. cornuta*, the bandings on the abdomen are obscure, and there is no large spot on the last abdominal somite (Figs 7a, b; see also Hayashi 1986; Hsu and Chan 2023).

Although *P. cornuta* has been reported from India (Chanda 2016b; Muthu 1968), the original description of *P. maxillipedo* described from India and Myanmar clearly mentioned that this species has more rostral teeth (8–10 excluding epigastric tooth), a postrostral carina as "… continued right up to the posterior border of the carapace, is sharp and particularly prominent…," the pereiopod III bearing a big basial spine, and the middle of the posterior plate of the thelycum with "…a globous tubercle…" (Alcock 1906). The present Indian specimens with characteristics described in the previous paragraph fit well with the original description of *P. maxillipedo* and can be considered as typical of this species. As the basial spine is occasionally absent or small at the pereiopod III in *P. maxillipedo*, the records of *P. cornuta* from India based only on males (Chanda 2016b; Muthu 1968) become doubtful. Even those Indian records of *P. cornuta* represent a species different from *P. maxillipedo*; there are possibilities that they may be *P. amicus* or *P. incisa* because these two species also lack a basial spine at the pereiopod III, and the latter species has recently been suggested to occur off Bangladesh (Fakhruddin et al. 2024).

Actually, most of the characters used in separating *P. maxillipedo* from *P. cornuta* can also be applied to distinguish it from *P. amicus* or *P. incisa* (Table 2). *Parapenaeopsis maxillipedo* is unique in the "*P. cornuta*" species group as it has the postrostral carina distinct along the entire length (Fig. 2b) and likely also in its coloration (Fig. 7c, *P. incisa* still without information on coloration but probably similar to *P. cornuta* and *P. amicus*). Moreover, *P. maxillipedo* differs from the other species of the "*P. cornuta*" group by generally having more rostral teeth (Fig. 1b), longer postrostral carina (Figs 1b, 2b), bearing a large basial spine at the pereiopod III (Fig. 6b), and posterior plate of thelycum having a high median boss (Fig. 5b). Nevertheless, the petasma and endopod of pleopod II in males are almost identical between *P. maxillipedo* and *P. cornuta* (Figs 3a, b, 4a, b). The thelycum of these two species is also rather similar, but with the median boss at the posterior plate more developed and the anterior plate somewhat more elongated (0.79–1.03, avg. 0.91 as long as wide) in *P. maxillipedo* (Fig. 5b; vs. 0.74–0.95, avg. 0.85 as long as wide in *P. cornuta*, Fig. 5a).

Although *P. maxillipedo* has been reported from India to the Philippines and tropical Australia (see Chan

Table 2. Distinguishing characters amongst the species of the "*Parapenaeopsis cornuta*" group. Those in bold are unique characteristics for that species, while those in red are rather subtle and more difficult to perceive.

	P. cornuta	***P. maxillipedo***	***P. amicus***	***P. incisa***
Rostrum extending to	distal antennular segment and often reaching tip of antennular peduncle	base and middle of distal segment of antennular peduncle	around tip of second segment of antennular peduncle	distal antennular segment or just overreaching antennular peduncle
Dorsal teeth (excluding epigastric tooth)	6–8, avg. 7.0	8–10, avg. 8.9	7–9, avg. 7.8	6–8, avg. 7.0
Postrostral carina	0.72–0.92, avg. 0.85 carapace length, posterior 1/4 broadened and obscure	**0.91–0.97, avg. 0.96 carapace length, entire length similar width, and distinct**	0.77–0.89, avg. 0.85 carapace length, posterior 1/4 broadened and obscure	0.77–0.89, avg. 0.84 carapace length posterior 1/4 broadened and obscure
Pereiopod III basial spine	usually absent, rarely present only in males	**usually present**	always absent	always absent
Male pleopod II endopod	greatly modified and boot-like, distal margin medially straight or concave	greatly modified and boot-like, distal margin medially straight or concave	**normal, sword-like**	greatly modified and boot-like, **distal margin medially protruded and convex**
Petasma, tip of horn-like distolateral projection	with distinct protuberance only at outer side	with distinct protuberance only at outer side	**distinctly protruded at both sides and hammer-like**	**bifurcate, no lateral protuberance**
Thelycum anterior plate	semi-quadrate, 0.74–0.95, avg. 0.85 as long as wide, rarely with median longitudinal furrow	semi-quadrate, 0.79–1.03, avg. 0.91 as long as wide, median longitudinal furrow absent	**semicircular, 0.59–0.73, avg. 0.65 as long as wide, with median longitudinal furrow**	**rectangular with lateral margins concave, 0.99–1.17, avg. 1.09 as long as wide,** median longitudinal furrow absent
Thelycum posterior plate median part	**weakly elevated into a weak median ovate boss**	**highly elevated into a distinct median ovate boss**	**surface sunken**	**surface flattened**
Tuft of hairs behind thelycum	thick and long, bluish in color	thick and long, bluish in color	**thin and short, colorless**	thick and long, color unknown
Coloration	abdomen slightly banded, last somite without special markings	**abdomen distinctly banded, last somite bearing large dark posterolateral spot with anterior thick white margin**	abdomen slightly banded, last somite without special markings	color unknown

1998; Holthuis 1980, 1984; Pérez Farfante and Kensley 1997), the present study is only able to verify its distribution in India, Thailand, and Malaysia. Materials of this species from India and Malaysia are here examined. The color photograph of *P. maxillipedo* from Thailand given by Chaitiamvong and Supongpan (1992: pl. 43) shows the characteristic large back spot on the last abdominal somite of this species. The drawings of *P. maxillipedo* in the FAO species identification guides for the Western Indian Ocean (Holthuis 1984), Sri Lanka (De Bruin et al. 1995), Myanmar (Psomadakis et al. 2019), Western Central Pacific (Chan 1998) also showed clearly the characteristic large dark spot with an anterior thick white margin on the last abdominal somite. On the other hand, the Philippine material reported as "*P. maxillipedo*" by Motoh and Buri (1984) was described as the basial spine at the pereiopod III sometimes small in females and the bands on the abdomen wider, but the characteristic large dark spot at the last abdominal somite was absent in their illustrated line-drawing (Motoh and Buri 1984: fig. 71). The Australian material reported as "*P. cornuta maxillipedo*" by Racek and Dall (1965) was also described as having the basial spine at the pereiopod III much reduced, like in some females from New Guinea (see also Racek and Yaldwyn 1971). Re-examination of the Philippines, New Guinea, and Australian material will be necessary to understand the exact eastern geographical range of *P. maxillipedo*.

Parapenaeopsis amicus V. C. Nguyên, 1971

Figs 1c, 2c, 3c, 4c, 5c, 7d

Parapenaeopsis amicus V. C. Nguyên 1971: 46, fig. 1 (type locality: West Tonkin Gulf); Hsu and Chan 2023: 222, figs 1, 6a.

Parapenaeopsis sinica Liu and Wang 1986: 214 (nomen nudum), 1987: 527, fig. 4. (type locality: Wailuo, Guangdong, China); Liu and Zhong 1988: 212, fig. 131, pl. 3: 4, 5: 6.

Kishinouyepenaeopsis amicus – De Grave and Fransen 2011: 215.

Material examined. Taiwan • [NTOU M02365]: Yilan County, Dasi fishing port, commercial trawler, 17 Jul. 1984, 1♀, cl 26.6 mm • [NTOU M02366]: Hsinchu City, Nanliao fishing port, commercial trawler, 4 Jul. 1984, 1♀, cl 31.1 mm

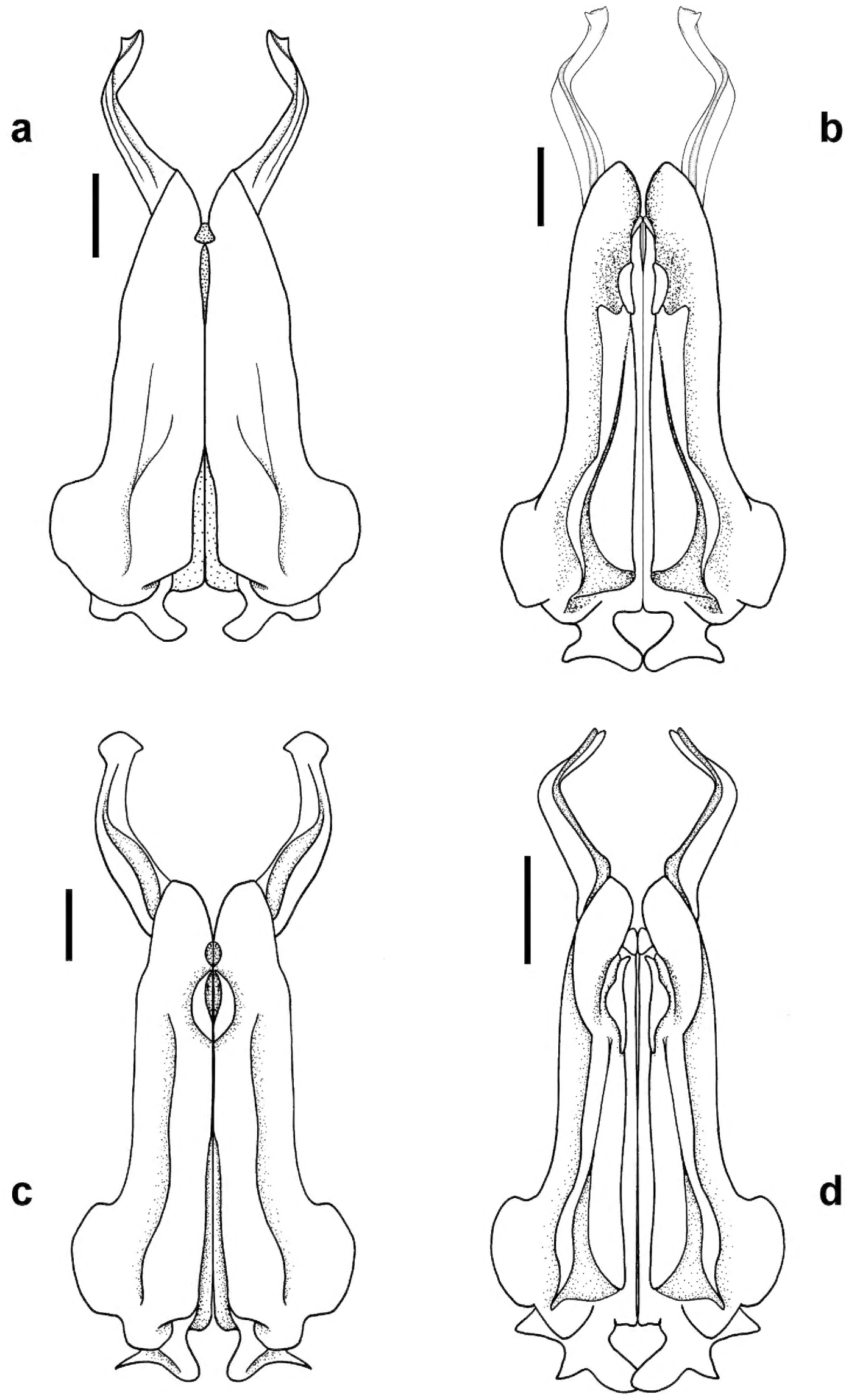

Figure 3. Petasma, ventral view. **a.** *Parapenaeopsis cornuta* (Kishinouye, 1900), Cijin, Kaohsiung City, Taiwan, male cl 18.8 mm (NTOU M02363). **b.** *P. maxillipedo* Alcock, 1906, Strait of Malacca, Pantai Remis, Perak, Malaysia, male cl 22.5 mm (USM_INV 1009). **c.** *P. amicus* V. C. Nguyên, 1971, Budi fishing port, Chiayi County, Taiwan, male cl 26.0 mm (NTOU M02372), modified from Hsu & Chan, 2023. **d.** *P. incisa* Wang & Liu in Liu and Wang 1987, Sanya, Hainan, Southern China, males cl 14.9 mm (MBM 155044). Scale bars: 1 mm.

• [NTOU M02367]: Changhua County, Wenzi fishing port, commercial trawler, 5 Aug. 2021, 16♂♂, cl 17.5–22.3 mm, 18♀♀, cl 18.4–25.0 mm • [NTOU M02368]: Yunlin County, Mailiao, Jul. 2009, 12♂♂, cl 11.4–17.6 mm, 18♀♀, cl 13.0–22.5 mm • [NTOU M02369]: Yunlin County, Mailiao, 18 May 2010, 2♂♂, cl 23.0–24.3 mm, 1♀, cl 28.4 mm • [NTOU M02418]: Chiayi County, Budai fishing port, commercial trawler, 26 May 1974, 3♂♂, cl 15.6–26.9 mm, 1♀, cl 30.5 mm • [NTOU M02370]: Chiayi County, Budai fishing port, commercial trawler, 20 Jan. 1995, 4♂♂, cl 18.1–21.5 mm, 2♀♀, cl 18.4–20.1 mm • [NTOU M02371]: Chiayi County, Budai fishing port, commercial trawler, 5 Feb.

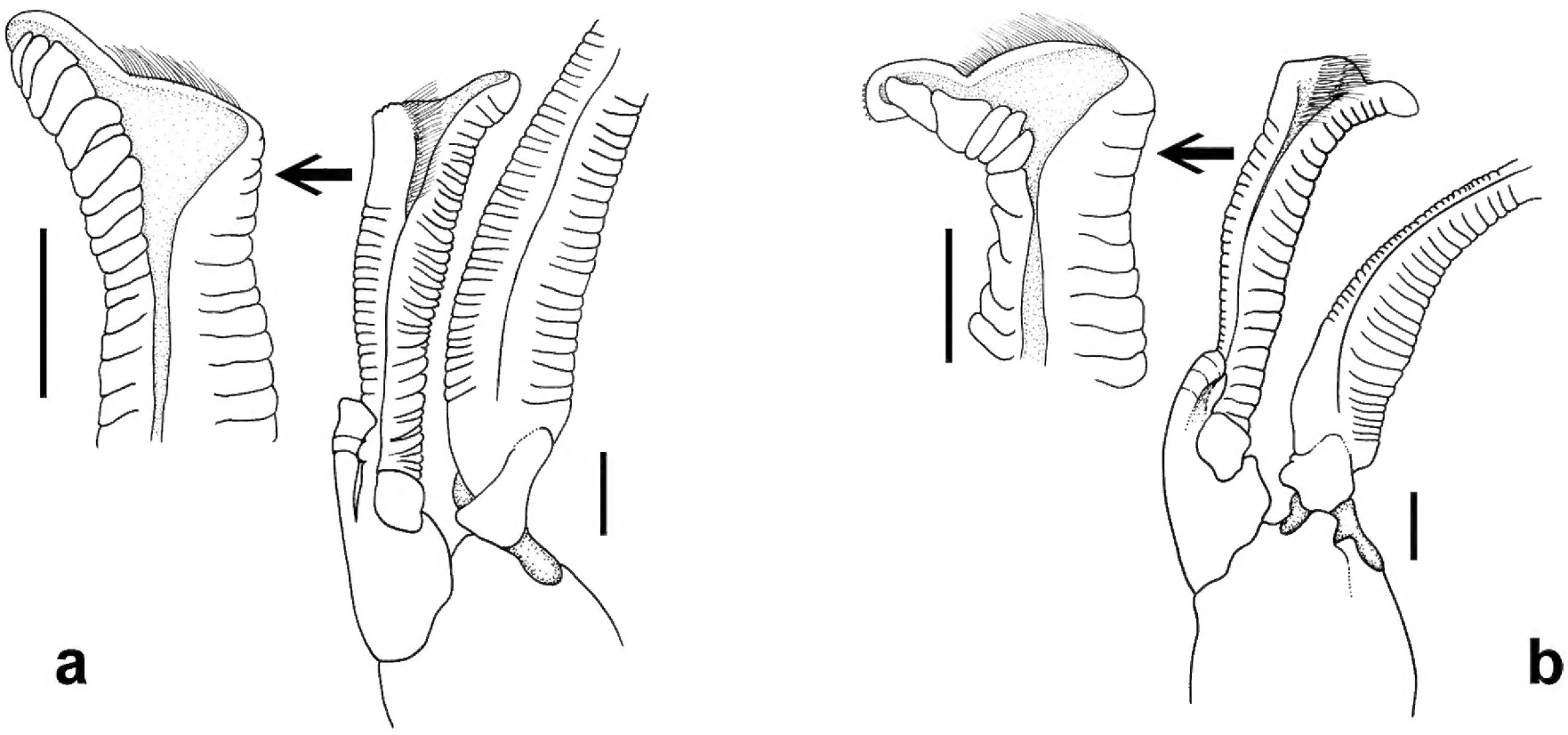

Figure 4. Right pleopod II endopod and basal part of exopod, dorsal view, and only thick, stiff setae shown. Magnified distal part of endopod in **a**, **b**, **d** in ventral view. **a.** *Parapenaeopsis cornuta* (Kishinouye, 1900), Cijin, Kaohsiung City, Taiwan, male cl 18.8 mm (NTOU M02363). **b.** *P. maxillipedo* Alcock, 1906, Strait of Malacca, Pantai Remis, Perak, Malaysia, male cl 22.5 mm (USM_INV 1009). **c.** *P. amicus* V. C. Nguyên, 1971, Budi fishing port, Chiayi County, Taiwan, male cl 26.0 mm (NTOU M02372), modified from Hsu & Chan, 2023. **d.** *P. incisa* Wang & Liu in Liu and Wang 1987, Sanya, Hainan, Southern China, males cl 14.9 mm (MBM 155044). Scale bars: 1 mm.

2000, 20♂♂, cl 15.1–22.7 mm, 20♀♀, cl 15.3–23.4 mm • [NTOU M00762]: Chiayi County, Budai fishing port, commercial trawler, 2 Jul. 2002, 8♂♂, cl 26.5–29.2 mm, 10♀♀, cl 22.5–33.2 mm • [NTOU M02372]: Chiayi County, Budai fishing port, commercial trawler, 8 Feb. 2021, 21♂♂, cl 22.2–26.0 mm, 21♀♀, cl 23.1–31.1 mm • [NTOU M02417]: Chiayi County, Budai fishing port, commercial trawler, 12 Dec. 2021, 2♀♀, cl 26.3–29.5 mm • [NTOU M02373]: Kaohsiung City; 10 Mar. 1975, 1♂, cl 24.4 mm, 1♀, cl 29.2 mm • [NTOU M02374]: Pingtung County, Donggang fishing port, commercial trawler, 5 Mar. 2021, 2♂♂, cl 24.5–25.0 mm, 1♀, cl 28.4 mm • [NTOU M02375]: Penghu County, Third fishing port, commercial trawler, Jun.–Aug. 2013, 3♀♀, cl 24.1–36.6 mm.

Diagnosis. Rostrum horizontal straight with tip recurved upwards, armed with 7–9 (avg. 7.8, n = 20, excluding epigastric tooth) teeth along dorsal border except near tip, extending to around tip of second segment of antennular peduncle. Postrostral carina with posterior 1/4 broadened and obscure, often with weak median pit, extending posteriorly to 0.77–0.89 (avg. 0.85, n = 20) of carapace length. Longitudinal suture short, extending posteriorly to about level of epigastric tooth. Pereiopods I and II bearing basial spines and epipods, pereiopod III lacking basial

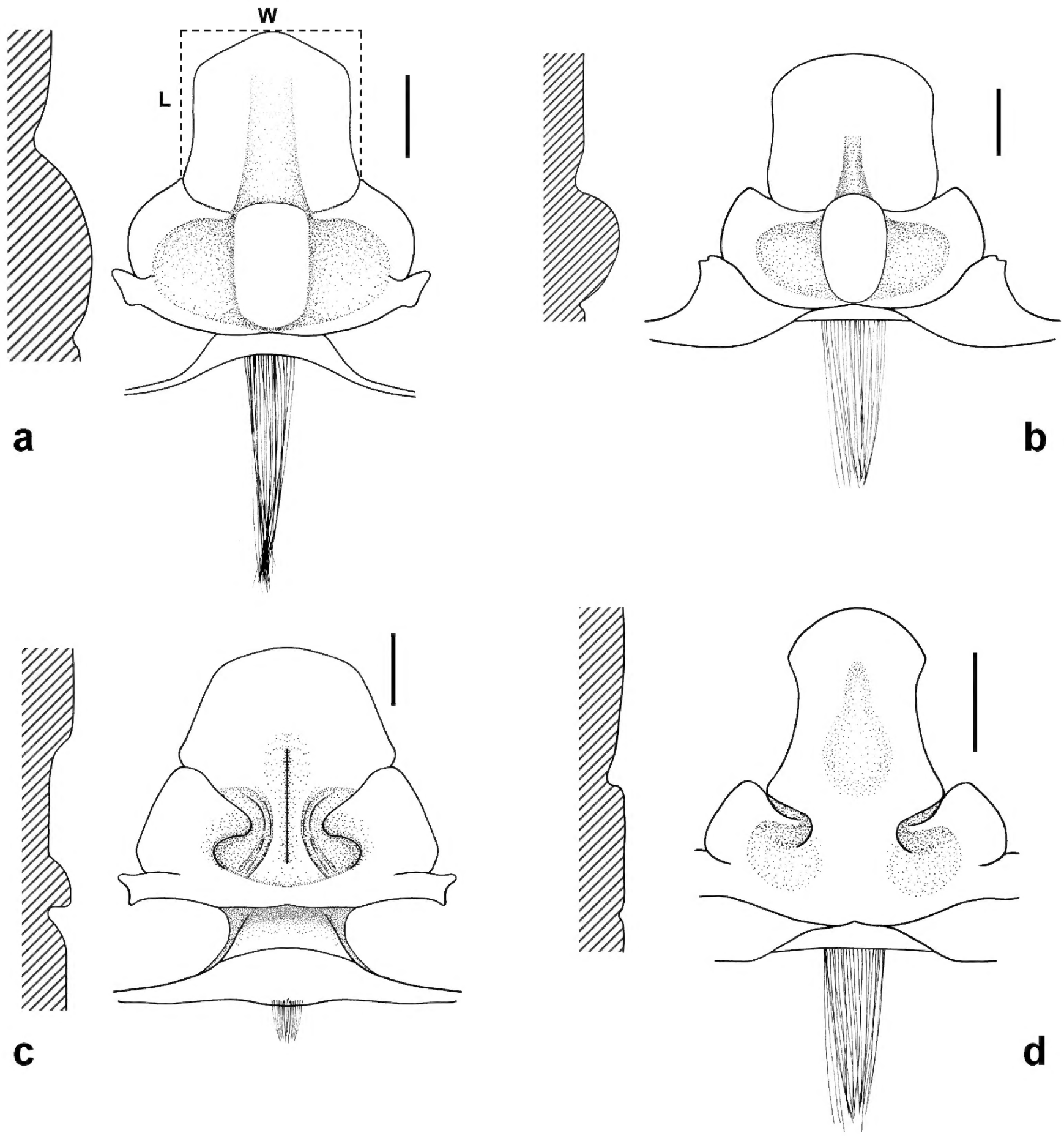

Figure 5. Thelycum, ventral view. Adjacent shading figure representing lateral cross-section along midline. **a.** *Parapenaeopsis cornuta* (Kishinouoe, 1900), Cijin, Kaohsiung City, Taiwan, female cl 22.4 mm (NTOU M02363). **b.** *P. maxillipedo* Alcock, 1906, Strait of Malacca, Pantai Remis, Perak, Malaysia, female cl 26.8 mm (USM_INV 1011). **c.** *P. amicus* V. C. Nguyên, 1971, Budi fishing port, Chiayi County, Taiwan, female cl 27.3 mm (NTOU M02372). **d.** *P. incisa* Wang & Liu in Liu and Wang 1987, Sanya, Hainan, Southern China, females cl 17.6 mm (MBM 155044). L: anterior plate length; W: anterior plate width. Scale bars: 1 mm.

spine. Abdominal somites I and II without dorsal carina. Telson lacking movable lateral spinules. Males with endopod of pleopod II normal in shape, sword-like as exopod; petasma with distolateral projections elongated and horn-like, tip of horn distinctly protruded on both sides (outer protrusion often larger) and hammer-like. Female thelycum with anterior plate shovel-like to semicircular (more often), 0.59–0.73 (avg. 0.65, n = 10) as long as wide, surface sunken with distinct median longitudinal furrow extending to posterior plate; posterior plate with median part also sunken, lateral parts as 2 large semicircular processes; tuft of setae behind posterior plate short and thin.

Coloration. (Fig. 7c) Similar to *P. cornuta* except tuft of short setae behind thelycum colorless. Color photograph of this species given in Hsu and Chan (2023).

Distribution. Known with certainty from Vietnam to southern China and Taiwan, intertidal to about 50 m deep (Liu and Wang 1987; Liu and Zhong 1988).

Remarks. Although the general appearance of *P. amicus* is very similar to the other members of the "*P. cornuta*" species group, it can be readily distinguished by the shape of genitalia. For males, *P. amicus* is unique in having a normal pleopod II endopod (Fig. 4c; v.s. greatly modified and boot-like, Figs 4a, b, d). In females, the tuft

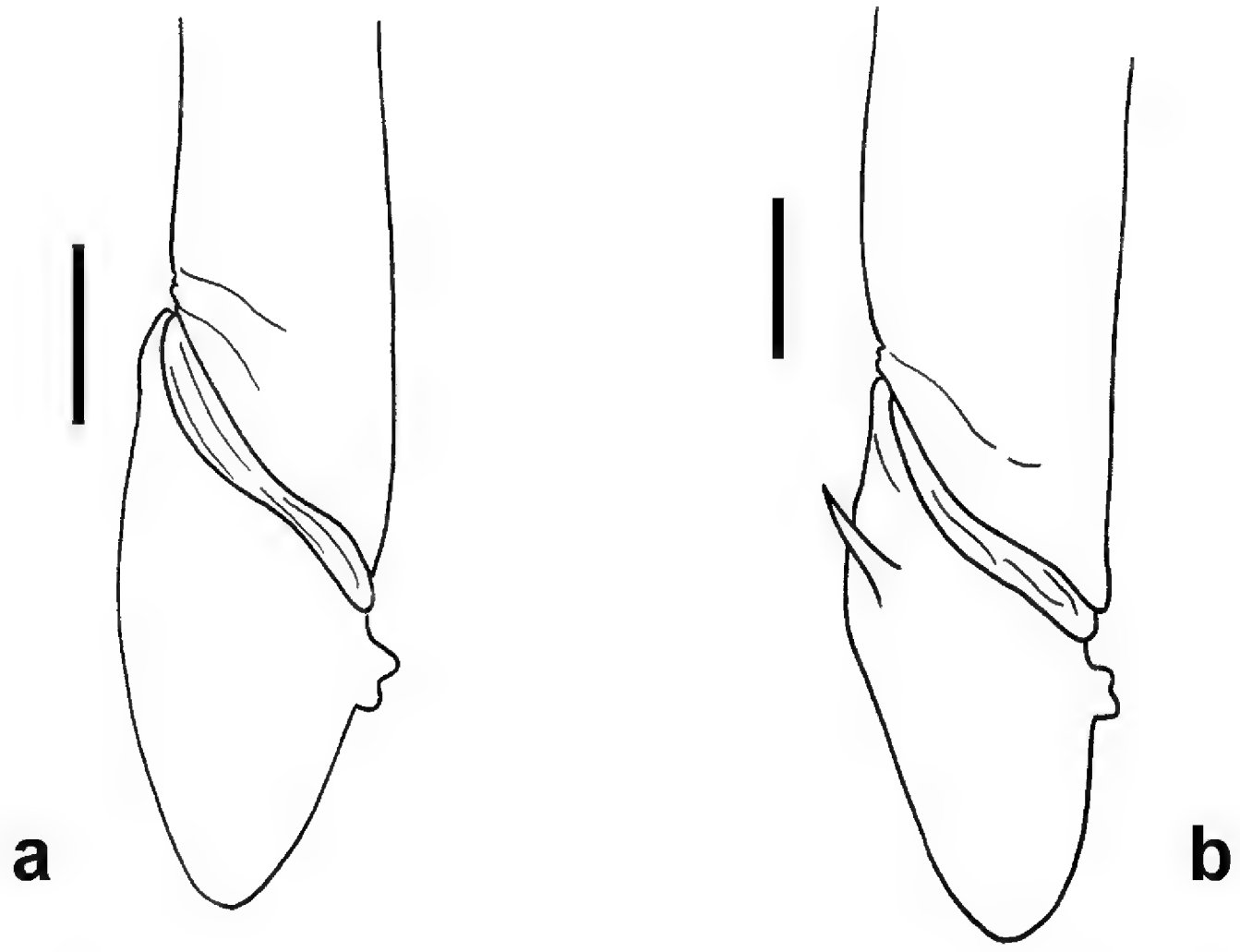

Figure 6. Left pereiopod III basis and proximal part of ischium, lateral view. **a.** *Parapenaeopsis cornuta* (Kishinouye, 1900), Cijin, Kaohsiung City, Taiwan, female cl 22.4 mm (NTOU M02363). **b.** *P. maxillipedo* Alcock, 1906, Strait of Malacca, Pantai Remis, Perak, Malaysia, female cl 26.8 mm (USM_INV 1011). Scale bars: 1 mm.

Figure 7. a. *Parapenaeopsis cornuta* (Kishinouye, 1900), Keelung City, Taiwan, male cl 14.5 mm (NTOU M02357), from Hsu & Chan, 2023 (reproduced with permission from the copyright holder). **b.** Fishery catch mainly composed of *P. cornuta*, Toyohama fish market, Aichi Prefecture, Japan (photographed by T. Nakano). **c.** *P. maxillipedo* Alcock, 1906, Tuticorin fishing harbor, Tamil Nadu, India, female cl 19.0 mm (NTOU M02626). **d.** *P. amicus* V. C. Nguyên, 1971, Budi fishing port, Chiayi County, Taiwan, female cl 29.5 mm (NTOU M02417), from Hsu & Chan, 2023 (reproduced with permission from the copyright holder).

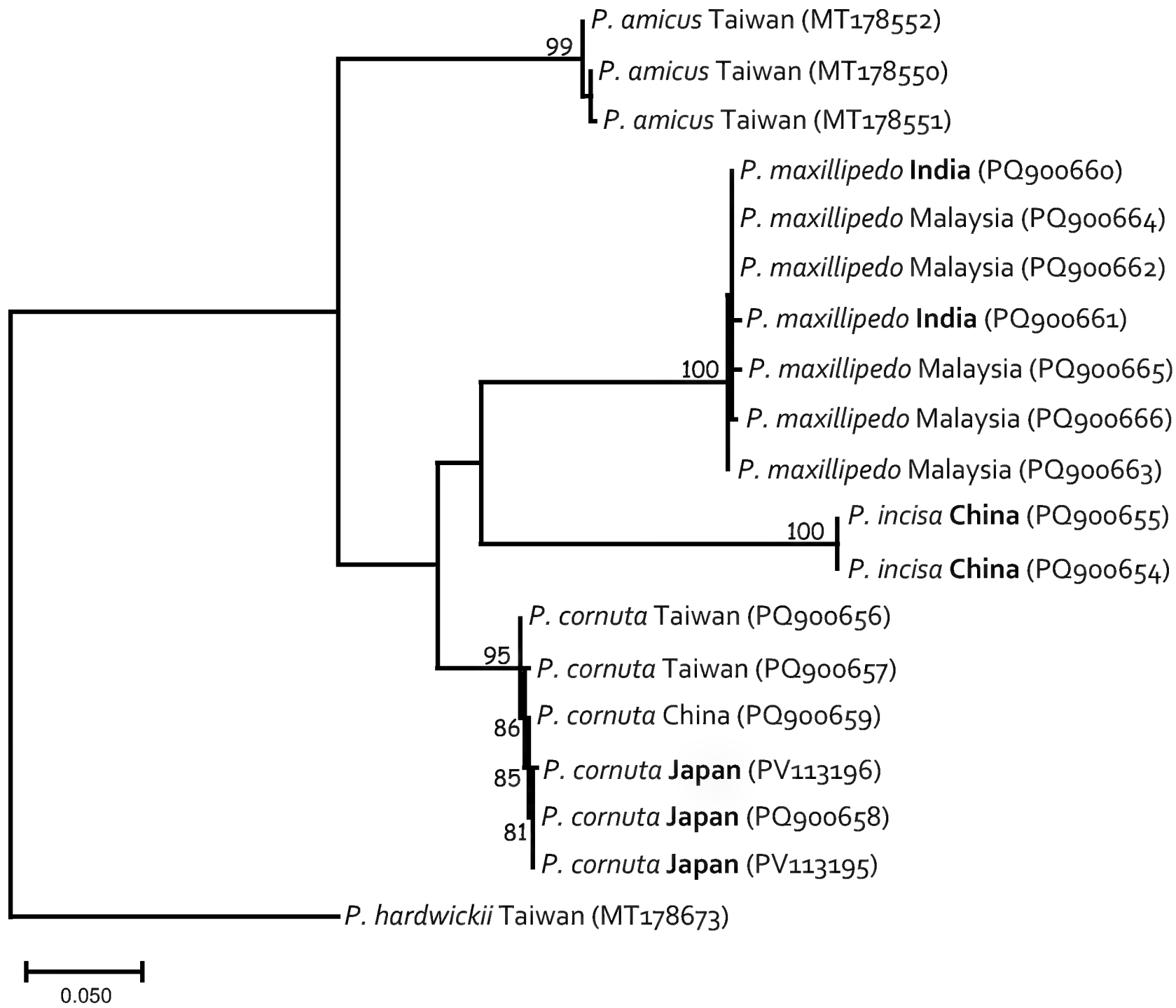

Figure 8. Maximum-likelihood tree (TIM2+G4+F model) amongst the species of the "*Parapenaeopsis cornuta*" group based on the DNA barcode gene mtCOI (615 bp) sequences generated from this work plus three sequences of *P. amicus* from Taiwan used in Hurzaid et al. (2020) and with specimens re-examined. *Parapenaeopsis hardwickii* was used as an outgroup. Numbers at nodes represent bootstrap support; values below 80 are not shown. Bold: type-locality.

of setae behind the thelycum is thin and short (Fig. 5c; v.s. thick and long, Figs 5 a, b, d). Efforts to locate the types of *P. amicus* were unsuccessful (personal communication from Tran Anh Duc). As both *P. amicus*, described from Vietnam (V. C. Nguyên 1971: fig. 1B), and *P. sinica* Liu & Wang, 1987, described from southern China (Liu and Wang 1987: fig. 4e; Liu and Zhong 1988: fig. 131–5), have the characteristic short and thin setae behind the thelycum, they are determined to be synonyms.

Besides the pleopod II endopod in males and tuft of setae behind the thelycum in females, *P. amicus* can also be separated from the other species of the group by some subtle differences in the genitalia (Table 2). The tip of the horn-like petasma has both sides distinctly protruded and hammer-like in *P. amicus* (Fig. 3c), but only with the outer side protruded in *P. cornuta* (Fig. 3a) and *P. maxillipedo* (Fig. 3b) or both sides not protruded in *P. incisa* (Fig. 3d). In *P. amicus*, the thelycum has a median longitudinal furrow, the anterior plate is relatively short (0.59–0.73, avg. 0.65 as long as wide), and the posterior plate medially sunken (Fig. 5c). For the other species of the "*P. cornuta*" group, the thelycum (Figs 5a, b, d) generally lacks a median longitudinal furrow (but is occasionally present in *P. cornuta*), the anterior plates are usually longer (0.74–1.17 as long as wide), and the median parts of the posterior plates are flattened (in *P. incisa*, Fig. 5d) to more or less protruding into a boss [low in *P. cornuta* (Fig. 5a) and high in *P. maxillipedo* (Fig. 5b)]. However, the characteristic shape of the genitalia is generally less developed in juveniles and young specimens. These subtle differences in genitalia are hence sometimes not useful to separate small individuals of this species group.

It is also found that the rostrum is relatively shorter, not reaching the tip of the antennular peduncle, in *P. amicus* (Fig. 1c) and *P. maxillipedo* (fig. 1b). In *P. cornuta* (Fig. 1a) and *P. incisa* (Fig. 1d), the rostrum is often extending to or even overreaching the tip of the antennular peduncle. Other differences previously proposed to distinguish *P. amicus* from the other species of the "*P. cornuta*" group [such as the number of rostral teeth, postrostral carina length, the presence of a median pit on postrostral carina, and setae on the branchiocardiac groove (Liu and Wang 1987; Liu and Zhong 1988; V. C. Nguyên 1971)] are found to be rather variable, with many overlappings.

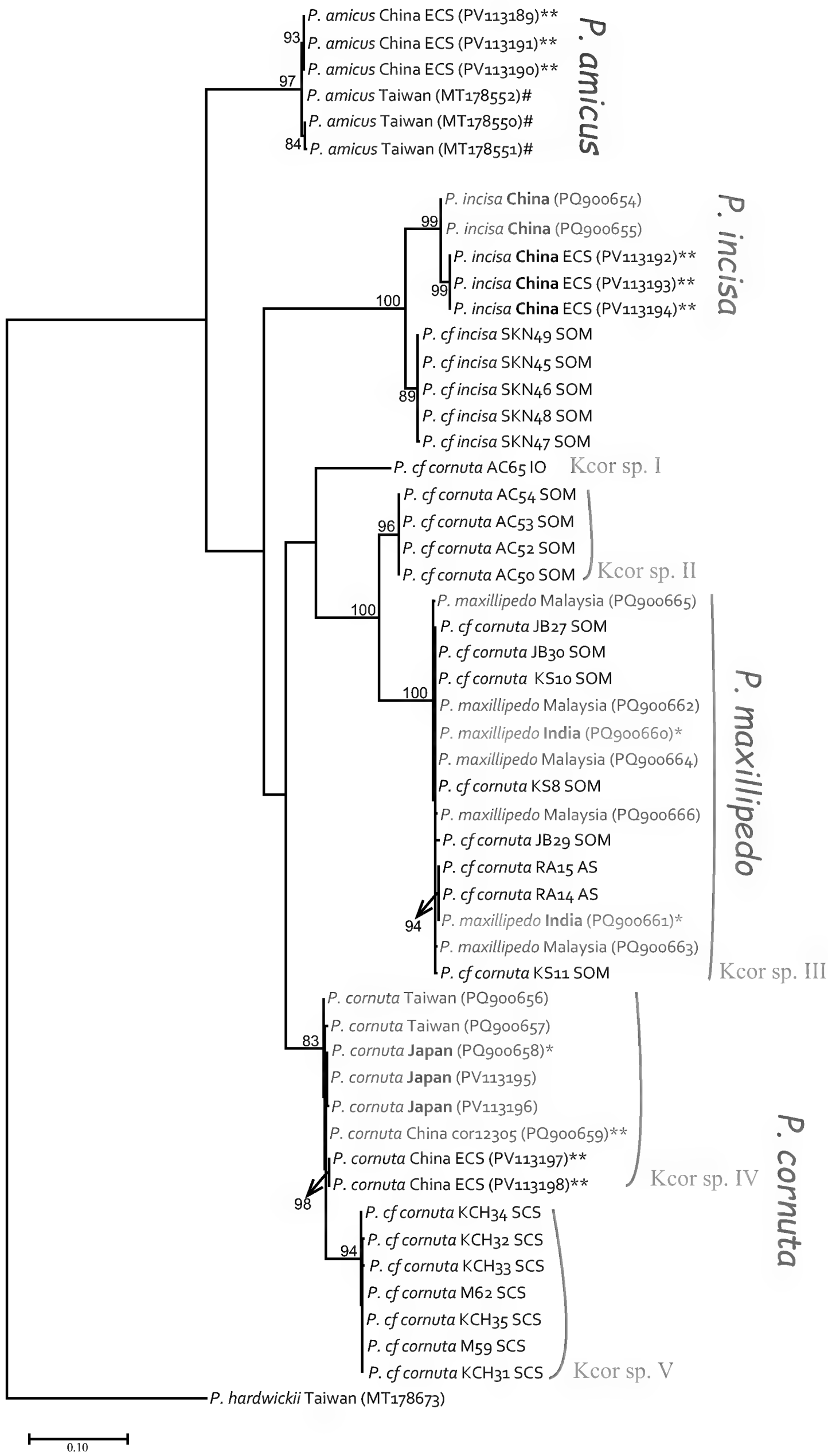

Figure 9. Maximum-likelihood tree (TIM2+G4+F model) amongst the species of the "*Parapenaeopsis cornuta*" group based on the DNA barcode gene mtCOI (615 bp) dataset in Hurzaid et al., 2020: fig. 3 plus the sequences generated in this work. *Parapenaeopsis hardwickii* was used as an outgroup. Numbers at nodes represent bootstrap support; values below 80 are not shown. Bold: type-locality; blue: sequences generated from this work; red: same specimens sequenced in Hurzaid et al. (2020) and the present work, but with different sequences and clade assignments. *Sequences generated from this work are from the same specimens used in Hurzaid et al. (2020). **Sequences used in Li et al. (2014). # Specimens re-examined in this work.

Molecular analysis also indicates that *P. amicus* is more distant from the other species of the "*P. cornuta*" group (Figs 8, 9, Table 1). However, the body color of *P. amicus* (Fig. 7d) is very similar to *P. cornuta* (Figs 7a, b) and very likely also with *P. incisa* (see Hsu and Chan 2023; Liu and Zhong 1988), rendering it difficult to determine its exact distribution from literature. At present, it can only be confirmed that *P. amicus* is distributed from Vietnam to eastern Guangdong in southern China and Taiwan (Hsu and Chan 2023; Liu and Wang 1987; Liu and Zhong 1988). Whether *P. amicus* has a wider geographical distribution will need re-examination of the material reported as "*P. cornuta*" in the various localities from India to Australia. For example, a recent study found that *P. amicus* is actually much more abundant than *P. cornuta* in Taiwan (Hsu and Chan 2023).

Parapenaeopsis incisa Wang & Liu in Liu & Wang, 1987

Figs 1d, 2d, 3d, 4d, 5d

Parapenaeopsis incisa Liu and Wang 1986: 214 (nomen nudum); 1987: 525, fig. 3. (type locality: Wailuo, Guangdong, China); Liu and Zhong 1988: 210, fig. 130.

Kishinouyepenaeopsis incisa – De Grave and Fransen 2011: 216.

Material examined. **Southern China** • [MBM 155054]: Guangdong, Zhanjiang, Naozhou Island, 29 Jul. 1976, 1♀, cl 14.6 mm • [MBM 155041]: Hainan, Yinngehai, 55-K444, 7 Dec. 1955, 3♂♂, cl 14.5–14.8 mm, 3♀♀, cl 16.3–18.2 mm • [MBM 155057]: Hainan, Yinngehai, 57-K275, 26 Jun. 1957, 2♂♂, cl 12.9–14.4 mm, 2♀♀, cl 16.5–17.6 mm • [MBM 155044]: Hainan, Sanya, fish market, 90C-324, 25 Nov. 1990, 3♂♂, cl 13.2–14.9 mm, 3♀♀, cl 14.9–17.6 mm.

Diagnosis. Rostrum more or less horizontal, straight, and with tip recurved upwards, bearing 6–8 (avg. 7.0, n = 14, excluding epigastric tooth) teeth along dorsal border except near tip, extending to distal antennular segment or just overreaching antennular peduncle. Postrostral carina with posterior 1/4 broadened and obscure, sometimes with weak median pit, extending posteriorly to 0.77–0.89 (avg. 0.84, n = 17) of carapace length. Longitudinal suture short, extending posteriorly to about level of epigastric tooth. Pereiopods I and II with basial spines and epipods, pereiopod III without basial spine. Abdominal somites I and II with dorsal carina absent. Telson lacking movable lateral spinules. Males with endopod of pleopod II strongly modified and boot-like; medial part of distal margin protruded and convex, but concealed by tuft of dense long stiff setae arising from anterodistal part of endopod; petasma horn-like with distolateral projections strongly elongated, tip of horn more or less bifurcated and without lateral protuberances on both sides. Female thelycum with anterior plate elongated rectangular and lateral margins more or less concave, 0.99–1.17 (avg. 1.09, n = 9) as long as wide, surface slightly sunken; posterior plate with median part completely flattened, lateral parts semicircular; tuft of setae behind posterior plate long and thick.

Coloration. Not known, but likely similar to *P. cornuta* and *P. amicus*. The photograph of a fresh specimen from the Strait of Malacca, Malaysia, probably belongs to *P. incisa* (Fakhruddin et al. 2024: fig. 1; see Discussion); it has a color pattern very similar to *P. cornuta* and *P. amicus*, except with the body having more yellowish and greenish taints.

Distribution. Known with certainty from around Hainan Island in the South China Sea, intertidal to about 30 m deep (Liu and Wang 1987; Liu and Zhong 1988). Probably also distributed to the Strait of Malacca off Malaysia and Bangladesh (Fakhruddin et al. 2024; see Discussion).

Remarks. *Parapenaeopsis incisa* closely resembles *P. cornuta* and mainly differs in the shape of the genitalia. In males, the boot-like endopod of pleopod II has the median part of the distal margin protruded in *P. incisa* (Fig. 4d) but is straight or concave in *P. cornuta* (Fig. 4a). The tip of the horn-like petasma lacks a lateral protrusion in *P. incisa* (Fig. 3d) but is distinctly protruded on the outer side in *P. cornuta* (Fig. 3a). The thelycum of *P. incisa* has the anterior plate more or less rectangular and relatively long (0.99–1.17, avg. 1.09 as long as wide), while the median part of the posterior plate is completely flattened without any sign of elevation (Fig. 5d). In *P. cornuta*, the thelycum has the anterior plate semi-quadrate and relatively short (0.74–0.95, avg. 0.85 as long as wide), and the posterior plate bears a weak median ovate boss (Fig. 5a). These unique shapes of the genitalia are also useful in separating *P. incisa* from the other two species of the "*P. cornuta*" group (Table 2, Figs 3–5). Similar to the situation in *P. amicus*, other differences previously proposed to separate *P. incisa* from the other species of the "*P. cornuta*" group (Liu and Wang 1987; Liu and Zhong 1988) actually have many overlaps.

Although morphologically *P. incisa* is most similar to *P. cornuta*, the high genetic differences (COI sequence divergence 15.0–17.5%, Table 1) of *P. incisa* from the other species of the "*P. cornuta*" group well support its specific status. As *P. incisa* can only be satisfactorily distinguished from the other species of the "*P. cornuta*" group mainly by subtle differences in genitalia (Table 2), careful examination of the material reported as "*P. cornuta*" from various localities is necessary to determine the exact distribution of *P. incisa*.

Discussion

Of the four species in the "*P. cornuta*" species group, *P. cornuta* and *P. maxillipedo* are generally considered to have wide overlapping Indo-West Pacific distributions from India to the Philippines and Australia (see Chan 1998; Holthuis 1980; Pérez Farfante and Kensley 1997). The two other species, *P. amicus* and *P. incisa*, are thought to have rather restricted geographical ranges, with the former known from Vietnam to southern China and Taiwan (Hsu and Chan 2023), while the latter is found only in southern China (Liu and Zhong 1988). However, *P. incisa*

has recently been reported from Malaysia and Bangladesh (Fakhruddin et al. 2024). Although the present morphological and molecular comparisons validate the four nominal taxa in the "*P. cornuta*" species group (Fig. 8), the molecular genetic analysis of Hurzaid et al. (2020) indicated that there may be at least eight species in this group. Some specimens used for molecular analyses from Japan [CBM ZC3280], India [NTOU M02625] and *P. amicus* from Taiwan [NTOU M00762] are the same in the present analysis as in Hurzaid et al. (2020). A specimen [MBM 155074] of *P. cornuta* from southern China used in molecular analyses is also the same amongst Li et al. (2014), Hurzaid et al. (2020), and this work. However, the sequenced specimens from India [NTOU M02625] were assigned to *P. cornuta* by Hurzaid et al. (2020) but were determined to be *P. maxillipedo* in the present study. As such, there was a mistake in Hurzaid et al. (2020) in considering that both the Indian and Japanese materials belong to the same species and genetic clade (i.e., "Kcor sp. IV" in Hurzaid et al. 2020). The present Indian material actually belongs to the clade "Kcor sp. III" of Hurzaid et al. (2020). With this correction, the genetic analysis of Hurzaid et al. (2020) suggested the following (Fig. 9): there may be another species similar to *P. incisa* from the Strait of Malacca, or *P. incisa* has a wider distribution from southern China to at least the Strait of Malacca. *Parapenaeopsis cornuta* is at least distributed down to the southern part of the South China Sea off Malaysia (i.e., Mersing, Johor, and Kuching), with "Kcor sp. V" in Hurzaid et al. (2020) highly likely not representing a different species. On the other hand, *P. maxillipedo* is at least distributed from India to the Andaman Sea sides of Thailand (Ranong) and Indonesia (Lambeso, Aceh Jaya) as well as westward to the Strait of Malacca, or may need to be split into three species.

Another recent molecular analysis also suggested that *P. incisa* occurs in the Strait of Malacca and Bangladesh (Fakhruddin et al. 2024). However, the COI analyses by Fakhruddin et al. (2024: fig. 2) and Hurzaid et al. (2020: fig. 3) have different conclusions even though they are based on similar datasets. The Chinese and Strait of Malacca clades of "*P. incisa*" were determined to be separate and represented different species in Hurzaid et al. (2020). In contrast, the "*P. incisa*" materials from the Strait of Malacca and China were grouped in the same clade and mentioned as belonging to the same species with only "…a genetic distance of 0.5%..." between them in Fakhruddin et al. (2024). Re-analysis of the genetic distance between the single "Chinese" specimen (KR349256) and the abundant material (22 specimens) from the Strait of Malacca in Fakhruddin et al. (2024) reveals that there is actually a 4.94–5.34% sequence divergence in the COI gene (600–615 bp) between the specimens from these two localities. Moreover, this single "Chinese" COI sequence used in Fakhruddin et al. (2024) is from unpublished data on GenBank with its locality not specified and with a 1.38% difference from the sequences of the three Chinese specimens analyzed in Hurzaid et al. (2020; same sequences in Li et al. 2014). On the other hand, the result of 16S analysis in Fakhruddin et al. (2024: fig. 3) showing materials of "*P. incisa*" from different localities represented different genetic clades is more in collaboration with the conclusion of Hurzaid et al. (2020). Their "Chinese" 16S sequence (KR781021) is also based on unpublished data with its locality not specified on GenBank as well as their 16S sequence from Bangladesh (ON264685). Re-analysis of the 16S data in Fakhruddin et al. (2024) shows a sequence divergence as high as 2.57–3.07% (475 bp) amongst the material from China, the Strait of Malacca, and Bangladesh, suggesting that these populations may each represent a separate species. Examination of more material of the "*P. cornuta*" species group from various Indo-West Pacific localities using the following key and distinguishing characters defined in this work (Table 2) is necessary to fully understand the diversity and geographical distribution of each species in this group of commercial shrimp.

Key to the species of the "*Parapenaeopsis cornuta*" group

1 Postrostral carina distinct and of similar width along entire length, posterior end less than 1/10 carapace length from posterior margin of carapace; pereiopod III usually armed with basial spine; abdomen distinctly banded and with last somite bearing large white margined dark posterolateral spot ..... *P. maxillipedo*

– Postrostral carina with posterior 1/4 broadened and obscure, posterior end more than 1/10 carapace length from posterior margin of carapace; pereiopod III usually lacking basial spine; abdomen not distinctly banded and last somite without special markings* 2

2 Males with endopod of pleopod II normal and sword-like; females with tuft of hairs behind thelycum short and colorless, thelycum bearing median longitudinal furrow and with posterior plate medially sunken ..... *P. amicus*

– Males with endopod of pleopod II greatly modified and boot-like; females with tuft of hairs behind thelycum long and bluish*, thelycum usually lacking longitudinal furrow and with posterior plate medially flattened or elevated 3

3 Males with distal margin of endopod of pleopod II medially convex, tip of petasma lacking lateral protuberance; female thelycum with anterior plate 0.99–1.17 times as long as wide and lateral margins concave, posterior plate medially flattened ..... *P. incisa*

– Males with distal margin of endopod of pleopod II medially straight or concave, tip of petasma bearing distinct outer protuberance; female thelycum with anterior plate 0.74–0.95 times as long as wide and lateral margins not distinctly concave, posterior plate having a weak median ovate boss ..... *P. cornuta*

* Exact coloration of *P. incisa* still unknown.

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